NASA TECHNICAL TRANSLATION NASA TT F-11,466

NASA TT F-11,466

ON METHODS FOR THE DETERMINATION OF THE RESPIRATORY QUOTIENT DURING REST AND WORK

E. H. Christensen and O. Hansen

Translation of "Zur Methodik der Respiratorischen Quotient-Bestimmungen in Ruhe und bei Arbeit" Skandinavisches Archiv fur Physiologie, Vol. 81, pp. 137-179, 1939

NATIONAL AERONAUTICS AND SPACE ADMINISTRATION
WASHINGTON, D.C. 20546 FEBRUARY 1968

I.[1]

ON METHODS FOR THE DETERMINATION OF THE RESPIRATORY QUOTIENT DURING REST AND WORK

E. H. Christensen and O. Hansen**

ABSTRACT. Reliable determinations of the respiratory gas exchange in man may be of greatest significance in the laboratory and in the clinic. With untrained subjects one usually has to be content with the determination of the O_2-uptake since the CO_2- output, as measured in metabolic studies, frequently is a poor expression for the simultaneous CO_2-production so that a reliable interpretation of the experimental results is not possible. However, also the results of experiments with trained subjects may be afflicted with considerable errors in the case of poorly controlled experimental conditions. In the following we have attempted to demonstrate several of these sources of error with specific consideration of determinations during work and to discuss them. /137*

Methods

It is essential that determinations of the respiratory gas exchange employ methods which affect the normal regulation as little as possible. In the following we shall compare in various ways the Helmet Method of Hansen and Krogh (1935) (a modification of the Benedict Helmet) and the Douglas Method. In addition to that, the reliability of gas exchange determinations in the course of the working period shall be tested in greater detail.

The Helmet Method offers the same advantages as do experiments with /138

1. The following publications I through V represent a supplement to the earlier publications "Contribution to the physiology of severe muscular work." Skand. Arch. 1936, Suppl. Nr 10 to Vol. 74. Publication, among other things, was unfortunately delayed due to the sickness of Ove Hansen.

* Numbers in the margin indicate pagination in the foreign text.

** From the Laboratory for the Theory of Gymnastics and from the Laboratory of Zoophysiology of the University of Copenhagen.

the respiration chamber (as it was, for instance, used by Krogh and Lindhard [1920]). However, there are several reasons to prefer it over the latter: 1. the duration of individual periods of determination may be greatly shortened in the case of the Helmet Method since the system has a much smaller volume than a conventional respiration chamber. 2. each determination requires only one gas analysis. 3. blood samples may here be taken and, 4. temperature regulation is affected to a lesser extent since only the head of the subject is enclosed.

In the case of the Helmet Method, where the air is sucked through the system by means of a large gas meter of constant rate, the gas volume in the experiments here referred to was determined with an accuracy of 0.1 to 0.5%. The accuracy is poorest for maximum flow rates (approximately 800 liters/min.).

In cases in which the Douglas Method was applied in the first experimental series the expired air collected in rubber bags was in early experiments measured by a moist gas meter. It is difficult to establish a completely constant stream of air through the gas meter during the emptying process of these bags. This may under certain circumstances result in an error of 2 to 3% of the expiration volume. In subsequent experiments the bags were emptied with the help of a spirometer. It was thus possible to reduce the error in volume determinations to less than 1%. The speed of emptying in the case of the latter approach is very great.

In the Helmet Experiments the analytical apparatus of Krogh (1920) was used; it was thus possible to determine the O_2-difference with an accuracy of 0.2% and the CO_2-difference with an accuracy of 0.1% (details on the Helmet Method may be found in the publication of Hansen and Krogh [1935].

For the Douglas determinations the Haldane apparatus as modified by Krogh was used. In this case a skilled person may be able to establish an accuracy of approximately 0.5%.

Respiratory Changes Associated with the Apparatus

a) "Dead" Space

For the Helmet Method, as well as in the case of all chamber experiments, the CO_2-tension of the inspired air is increased as opposed to normal values. As a result of that a minor CO_2-rentention is observed, /139
as a rule, in the first few minutes after the start of an experiment. This increase in CO_2-tension is of lesser significance in the case of the Helmet Method than in the case of the earlier chamber method since the fresh air supply leads directly to the mouth of the subject.

The alveolar CO_2-tension is also increased in the case of Douglas determinations. This is due to the increased dead space by the addition of the valving system.

It is, however, possible to ascertain termination of the CO_2-retention by sufficiently long introductory periods prior to the actual periods of measuring (cf. Hansen and Krogh [1935]).

b) Exspiratory Resistance

In comparatory experimental series with the Helmet and Douglas Methods, a lower R.Q. was constantly found in Douglas experiments despite the application of rather long introductory periods. These observations are presented in Table 1.

Table 1. SUBJECT O.H. DETERMINATIONS 15-13 MINUTES AFTER THE START OF WORK

Work Intensity kgm/min.	R. Q.		Ventilation per liter O_2 Douglas determination	Remarks
	Helmet determination	Douglas determination		
1080	0.860	0.830	15.6	High Expiratory Resistance.
1260	0.862	0.830	14.1	
1440	0.867	0.815	15.3	

A systematic investigation was conducted in order to clarify these discrepancies. Part of the investigation consisted of varying the expiratory resistance. The determinations were carried out in part with the low resistance. A wide (30 mm), short (30 cm) piece of connecting tubing led to the Douglas bag, in part the connecting tube was a rubber hose free of bends (accordion wall hose) as is usually applied to metabolic studies. This hose had an inner diameter of 20 mm and a length of 1.5 m. The valve was in both experiments the same modified Enghoff-valve (Enghoff 1930). The intensity of work was 1260 kgm/min. in these experiments. This subject O.H. was used to perform metabolic determinations. Twenty minutes after the start of work the subject began respiration through the system of low resistance and after an initial period of 2 to 6 minutes, metabolic determinations were conducted; corresponding determinations were again carried out 50 minutes after the start of work. The average ventilation (0°, 760 mm) was in the case of these determinations 50 liter/min.; the O_2-uptake was 2.75 liter/min., the corresponding R.Q.-values may be seen from Fig. 1. Approximately 35 to 45 minutes after the start of work determinations were carried out in the same experiments with increased expiratory resistance. The initial period in these determinations was 0.5 to 8.5 minutes. The average ventilation was 46 liter/min., the O_2-uptake the same as before, the R.Q.-values may be seen from Fig. 1. /140

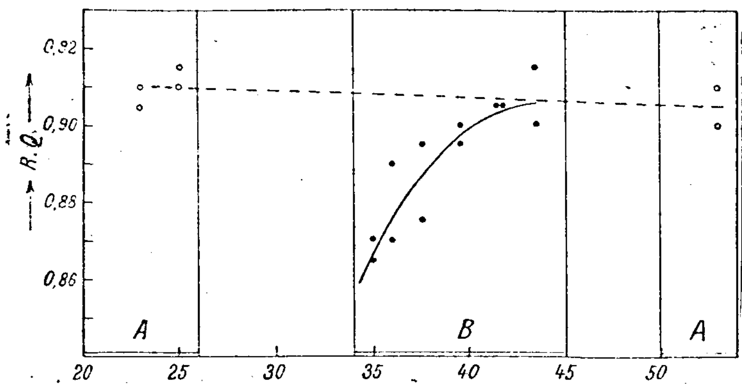

Fig. 1. Subject O.H. Intensity of Work 1260 kgm/min. (A) R.Q.-determinations at Low Expiratory Resistance 0 and (B) at Large Resistance .

The determinations at low resistance represent the normal decrease in R.Q. during the working period. The first values at increased expiratory resistance show an R.Q. of 0.87; upon continued valve respiration the R.Q. then approaches in the following 6-8 minutes the line of normal values. This means, that in the case of an insufficiently long initial period and at considerable resistance, the R.Q.-values are found to be too low for this subject.

The difference mentioned earlier between the R.Q.-values in the Helmet experiments and in the Douglas experiments (Tab.1), in all likelihood, was due to the increased ex-spiratory resistance in the Douglas experiments. The initial period was only approximately 2 minutes in these determinations and, as Table 1 shows, the ventilation per liter of O_2 was very low in this case; undoubtedly, there was a considerable hypoventilation and the R.Q.-values determined are too low.

From Fig. 1 it is, however, also clear that for sufficiently long initial periods, reliable R.Q.-values can be obtained also for high exspiratory resistance. Conclusions on the normal respiratory functions, such as ventilation volume and alveolar tensions are naturally not permitted from such experiments. /141

c) Untrained Subjects

In experiments during rest the exspiratory resistance in Douglas determinations is always very low for suitable experimental designs. Inspite of that, the respiratory functions may temporarily be strongly influenced, in particular in the case of untrained subjects. However, also subjects which had been trained earlier, frequently show changes in respiration during valve respiration if they have not breathed for a longer period of time through a valving system.

Table 2 shows the results with a subject of little training but with a sufficiently long initial period.

Table 2. SUBJECT F.G. 1932. DETERMINATIONS DURING REST

Date	R. Q. Helmet	R. Q. Douglas	R.Q.-R.Q. Douglas Helmet	Douglas Ventilation per liter O_2
21.10	0.832	0.830	0.00	21.8
24.10	0.865	0.880	+0.015	24.8
26.10	0.864	0.850	-0.015	23.4
28.10	0.822	0.815	-0.005	22.2
31.10	0.861	0.870	+0.01	22.9
7.11	0.823	0.810	-0.015	21.9
9.11	0.804	0.795	-0.01	20.0
	0.839	0.835	-0.005	22.6

Determinations according to Douglas were carried out on the same days following the Helmet experiments (initial period in the Helmet 15 minutes). The initial period in the Douglas experiments was approximately 10 minutes. Table 2 clearly indicates variations in ventilation; however, as a consequence of long initial periods, the R.Q.-values show deviations of a lesser extent and the good agreement with the R.Q.-values determined immediately before the Helmet experiments show that the values determined in Douglas experiments represent undoubtedly a reliable expression of the metabolic events.

In the case of completely untrained subjects, changes in ventilation as a consequence of valve respiration may be so pronounced that even in the case of an initial period of approximately 10 minutes no reliable R.Q.-values can be obtained.

Table 3. SUBJECT O.Bg. 1932. DETERMINATIONS DURING REST /142

Date	R. Q. Helmet	R. Q. Douglas	R.Q.-R.Q. Douglas Helmet	Douglas Ventilation per liter O_2
15.10	0.800	1.010	+0.20	42.5
18.10	0.838	0.730	-0.11	21.5
25.10	0.814	0.775	-0.04	20.5
27.10	0.820	0.860	+0.04	22.1
29.10	0.783	0.775	-0.01	20.6

The series of experiments reported in Table 3 corresponds to the experiments shown in Table 2 with the only difference that the subject O.Bg. was completely untrained. The first experiment on October 15 shows a pronounced hyperventilation and the determined R.Q. of 1.01 must be due to the fact that CO_2 was washed out strongly during the determination. The following Douglas determinations, despite approximately the same ventilations, show great variations in R.Q. In particular, the experiment of October 18 may be mentioned; here one finds for a normal ventilation of 21.5 liters per liter O_2 a subnormal R.Q.-value. This can undoubtedly be explained by the fact that during the initial period considerable hyperventilation and washing out of CO_2 took place and that during normal ventilation during the period of determination, now as a consequence of the subnormal alveolar CO_2-tension, a reduced CO_2-output is encountered.

The R.Q.-values of the Helmet experiments are also rather constant for this series of experiments and are likely to represent a reliable expression for the metabolic events.

Although metabolism may be increased in the case of untrained subjects, accidental changes in ventilation may influence the R.Q. so strongly that a reliable judgement becomes impossible.

Table 4. SUBJECT O.H. EARLY NOVEMBER OF 1931
INTENSITY OF WORK 1115 kgm/min. O_2-CONSUMPTION
APPROXIMATELY 2.8 liters/min.

Min. after the start of work	8	22	36	46	56
R.Q.	0.98	0.95	0.88	0.93	0.87
Ventilation per liter O_2	22.9	21.0	17.2	21.0	18.4

The initial period was in this as well as in subsequent experiments approximately 2 minutes; this is sufficient for trained subjects. The values for untrained subjects show, however, great variations in ventilation and in parallel with that changes in the R.Q. which are undoubtedly not due to qualitative changes in metabolism. /143

Table 5 shows experimental data with the same subject and at approximately the same work volume about one month later.

The values for the ventilation as well as those for the R.Q. are now considerably lower than earlier and show only minor variations. The R.Q.-values show only the usual decrease during the working period, which one finds for intensive work of long duration and are now in all likelihood a reliable expression for the metabloic events.

Table 5. SUBJECT O.H. AT THE END OF NOVEMBER 1931. WORK INTENSITY 1115 kgm/min. O_2-CONSUMPTION APPROXIMATELY 2.8 liters/min.

Min. after the start of work	18	40	60	95
R.Q.	0.85	0.82	0.83	0.82
Ventilation per liter O_2	18.8	18.3	18.2	18.2

On the basis of the experimental data just reported, we considered it essential for Douglas experiments with short initial periods to check the values obtained via this method by Helmet determinations. Therefore, in the same experiments, determinations with the Douglas Method and with the Helmet Method were carried out. Typical experimental data are compiled in Table 6.

Table 6. SUBJECT O.Bg. OCTOBER 20, 1932. WORK INTENSITY 720 kgm/min. O_2-CONSUMPTION 1.8 liters/min.

Min. after the start of work	23	29	36	
Method of determination	Helmet	Douglas	Helmet	
R.Q.	0.875	0.865	0.840	

SUBJECT O.Bg. OCTOBER 29, 1932 WORK INTENSITY 900 kgm/min. O_2- CONSUMPTION 2.2 liters/min.

Min. after the start of work	16	21	27	
Method of determination	Helmet	Douglas	Helmet	
R.Q.	0.944	0.935	0.908	

SUBJECT F.G. OCTOBER 28, 1932.
WORK INTENSITY 720 kgm/min. O_2-CONSUMPTION
1.9 liters/min.

Min. after the start of work	14	19	24	29
Method of determination	Douglas	Helmet	Douglas	Helmet
R.Q.	0.880	0.897	0.895	0.899

The established good agreement between the Douglas and Helmet values is certainly an expression for the fact that the R.Q.-values found are reliable. Since the initial period in the case of Douglas experiments was only approximately 2 minutes, we are entitled to assume that the ventilation is very close to normal values before the start of valve respiration and that in these experiments, consequently, conclusions with regard to the remaining respiratory functions are also possible. We have mentioned already earlier that also in the case of abnormal, however, constant respiration, reliable R.Q.-values may be obtained if only sufficiently long initial periods are allowed. However, in these case, conclusions on the normal respiratory functions were not possible.

Changes in Respiratory Functions at the Start of Work

Immediately after the start of work and in the case of greater work intensity the O_2-supply is inadequate and the energy processes in the working muscles proceed in part anaerobically. As a consequence of that an increased content in lactic acid may be found in blood, which in turn results in a corresponding CO_2-output and washing out of CO_2 by way of the expired air. Furthermore, in many instances ventilation is not momentarilly adjusted to the increased metabolism; the expired CO_2-volume is consequently not a measure for the CO_2-volume produced during the same period of time and the R.Q. found is not a reliable expression for the type of catabolic process.

If the work intensity is relatively low, the O_2-uptake will already after approximately 1 minute become adequate and the lactic acid content of blood will only be increased to a minor extent. A considerable increase in lactic acid usually occurs only in the case of work intensities which result in an O_2-consumption of 1.5 liters/min. or more.[3]

3. In dependence of the performance of the subject and the group of working muscles (for details cf. publication V).

With the subject O.Bg. of very little training we obtained, for instance, for a work intensity of 900 kgm/min. the following experimental data which may be seen from Fig. 2. Approximately 3 minutes after the start of work adequate O_2-uptake had been established.

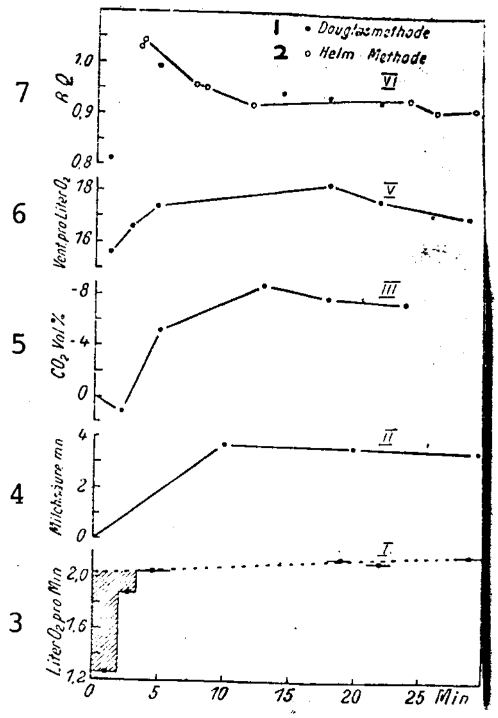

Fig. 2. Subject O.Bg. (little training). Work Intensity 900 kgm/min.
1. Douglas Method
2. Helmet Method
3. Liters O_2 per minute
4. Lactic acid mn.
5. CO vol.%
6. Ventilation per liter O_2
7. R.Q.

The O_2-uptake is 2.05 liter/min. /145 in the first few minutes and increases in the course of 30 minutes to 2.20 liters/min. (cf. later). The oxygen deficit of the first 3 minutes amounts to approximately 1.85 liters. The lactic acid in blood[4] showed an increase of approximately 3.5 millinormal and is 10 to 30 minutes after the start of work rather constant. The corresponding determinations of blood CO_2[5] do not show a decrease in CO_2-content during the first two minutes of work. After that, however, a decrease of approximately 8 volume % was observed. The first ventilation determination shows the minor ventilation of 15.5 per liter O_2; after approximately 5 minutes a level with a ventilation of approximately 17.5 liter O_2 was reached. The work determination, one minute after the start of work, showed an R.Q. of the same order as during rest, 3 to 4 minutes after the start of work, the R.Q. reaches a maximum value of approximately 1.03. Thereafter, a decrease /146 was observed and approximately 10 minutes after the start of work a normal value was reached.

For a work intensity of 1080 kgm/min., which results in an O_2-uptake of approximately 2.7 liters/min., the washing out of CO_2 was approximately 12 vol.% for the subject O.Bg., but also here an approximately steady state, as a rule, was reached approximately 15 minutes after the start of work.

---

4. Determinations by Bang (1936). For technical reasons it was not always possible to carry out all determinations on the same day. The reproductibility of the experiments was, however, so good, that the results of different experiments may be combined.

5. Determinations by Boje (1935).

Fig. 3 and 4 show experimental data obtained with the extensively trained subjects M.N. and O.B. Fig. 3 is the result of experiments with M.N., the work intensity was 1080 kgm/min.

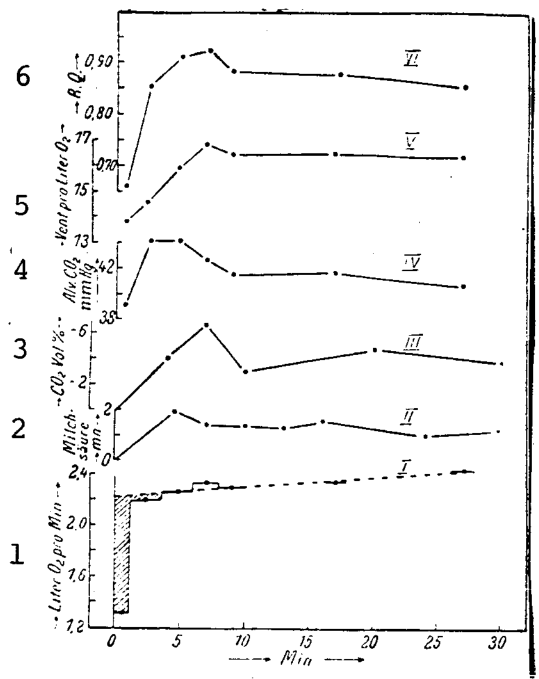

Fig. 3. Subject M.N. (well trained). Work Intensity 1080 kgm/min.

1. Liters of O_2 per min.
2. Lactic acid mn
3. CO_2 vol.%
4. Alveolar CO_2 mmHg.
5. Ventilation per liter O_2
6. R.Q.

Curve 1 shows the O_2-uptake in the course of the working period. As is evident from the curve, the O_2-uptake is adequate already 1 minute after the start of work, i.e., the O_2-uptake corresponds to the O_2-consumption. If in the course of the working period a minor increase in O_2-uptake occurs, then this is an expression for a decrease in efficiency (exhaustion, increased body temperature, etc.); the dashed line is a measure for the intensity of metabolism. As can be seen from the Figure the oxygen deficit is minor, only approximately 1 liter. Curve II shows the increase in lactic acid values for capillary blood as opposed to values during rest. The maximum increase, 2 millinormal, is reached approximately 5 minutes /147
after the start of work; subsequent values are lower. Curve III shows a corresponding decrease in CO_2-content in capillary blood. The lowest CO_2-content was found approximately 7 minutes after the start of work. On the average, the CO_2-content in these experiments is approximately 4 vol.% lower than the initial value during rest.

The increase in ventilation with regard to the O_2-uptake is reduced, as is indicated by curve V, which represents the ventilation per liter of O_2. Only approximately 7 to 8 minutes after the start of work, a level is reached for the ventilation. This reduced increase in ventilation is typical for the subject M.N.

Curve IV shows that the alveolar CO -tension is approximately 41 Hg for the steady state, i.e. approximately 3 mm Hg higher than the corresponding value during rest. During the first minute of work, the alveolar CO_2-tension is still relatively low with 39 mm Hg. Since the ventilation at this time is still low, we obtain subnormal values for the R.Q. Curve VI. The following determinations show a CO_2-tension of 44 mm Hg and for a still subnormal ventilation, now an approximately correct value is found for the R.Q. Approximately 4 to 8 minutes after the start of work the washing out of CO_2 takes place, since the ventilation becomes almost normal during this period and the alveolar CO_2-tension is simultaneously increased.

The other two trained subjects showed quite an analogous behavior. They only showed a faster increase in ventilation. During the first 10 minutes of work the washing out of CO_2 was only minor for these two subjects as a rule, at a work volume of 1080 kgm/min.

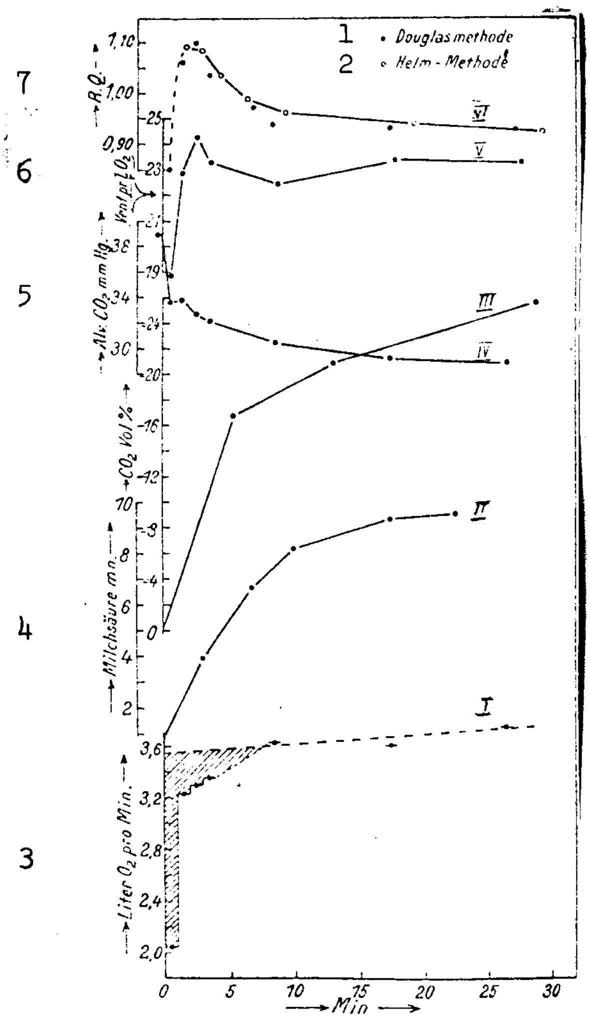

Fig.4. Subject O.B. (well trained). Work Intensity 1620 kgm/min.

1. Douglas Method
2. Helmet Method
3. Liters of O_2 per min.
4. Lactic acid mn
5. Alveolar CO_2 mm Hg
6. Ventilation per liter of O_2
7. R.Q.

For increasing work intensity the extensively trained subjects also show an increase in washing out of CO_2 and upon approximation of the maximum of the O_2-uptake, a steady state is no longer reached but washing out of CO_2 is continued until the end of the working period. The best trained subject O.H. was able to reach a steady state even for an O_2-uptake of approximately 4.1 to 4.2 liters/min. at a CO_2-reduction of the capillary blood of approximately 18 vol.%. The steady state was reached in the course of less than 10 minutes and the entire duration of work was 25 to 30 minutes. Subjects O.B. and M.N. were able to reach steady state still at an O_2-uptake of approximately 3.6 liters/min.

Fig. 4 is the result of an experiment with O.B.; the work intensity was 1620 kgm/min. After approximately 1 minute of work, the O_2-uptake is increased to approximately 3.25 liters/min. and in the course of the following 8 to 9 minutes a slow increase follows to approximately 3.65 liters/min.; only this O_2-uptake corresponds to the O_2-consumption. The O_2-deficit is therefore considerable, approximately 3.0 liters.

The corresponding curves for lactic acid in blood and CO_2 show that for these functions steady state can hardly be reached. The CO_2-determination 29 minutes after the start of work shows a decrease in the CO_2-content of the blood of approximately 25 vol.% for 4 liters of blood; this corresponds to one liter of CO_2 from blood. In the course of approximately 10 to 30 minutes after the start of work the respiratory functions show approximately steady state; the ventilation per liter of O_2 is here approximately 23 liters, the alveolar CO_2-tension is approximately 30 mm Hg and the R.Q. is approximately 0.94. As usual, the ventilation in the first minute of work is relatively low and simultaneously the R.Q. is also subnormal. During the subsequent period of washing out of CO_2 the R.Q. shows a maximum value of 1.10. /149

Discussion

The curves and tables reported illustrate the difficulties encountered during metabolic determinations, in particular during work; simultaneously they show, however, also the approaches that should be followed in order to obtain reliable information on metabolic processes for the so-called steady state during work. -- Under steady state we understand the period of work, 1. during which the O_2-uptake corresponds to the momentary O_2-requirement, 2. during which the respiratory functions have reached a level, 3. during which the CO_2-content and the lactic acid content of the blood are approximately constant and during which also the expired CO_2-amount corresponds to the CO_2-amount produced over the corresponding period of time. -- The steady state is certainly methodically most suitable for the elucidation of catabolic processes which are characteristic for a given work intensity at a given state of training. A second approach, for work of short duration and during which a steady state is not reached, during which, however, also the restitution phase after discontinuation of the work is taken into consideration, certainly provides in some instances reliable information on the metabolism during steady state. In certain instances, however, the results may also be misleading; this applies in particular to great work intensities. If one believes in calculating from the total R.Q. of the working period and the restitution the metabolism characteristic for a given work intensity, one then must make the assumption that the metabolic processes are the same for the entire period of work where, undoubtedly, the exygen uptake is inadequate and during which frequently a considerable production of lactic acid and accumulation of the same takes place in blood, the catabolic processes must be the same as later in the working period when the oxygen uptake is adequate and no detectable quantities of lactic acid are accumulating in blood. As long as one can not make these assumptions the "characteristic metabolism during work" will depend upon the duration of the period of work. For a short duration of work, the anaerobic period at the beginning of work will have a dominating influence, for work of longer duration, this period will be of lesser significance. /150

As has been shown by the experimental data each R.Q. determination during work should be checked with utmost care. The controls CO_2 and lactic acid determinations in blood as reported here simultaneously allow the conclusion that for good methods the determination of the catabolic processes is also possible for very great work intensity, approximately 10 to 15 minutes after the start of work. These determinations may be carried out with the Helmet Method as well as also with the much simpler Douglas Method.

Summary

During rest and during work comparative determinations of metabolism were carried out according to the Douglas Method as well as also with the Helmet Method as modified by Hansen and Krogh. In the case of untrained subjects, one sooner obtains reliable R.Q.-values with the Helmet Method rather than with the Douglas Method. For trained subjects, both methods are applicable; for reasons of greater simplicity, the Douglas method is to be preferred as a rule. For very great work intensities which require a ventilation of the lungs of 100 liters/min., it is of greatest significance for the application of the Douglas method, that all connections between the air passages of the subject and the Douglas method are as short as possible and as large in diameter as possible and that, in particular, the valves have wide openings. For narrow connections the expiratory resistance will become considerable, a factor that caused for the subjects studied here hypoventilation. Only for prolonged initial periods and for trained subjects is it possible to then obtain reliable R.Q.-values. Simultaneous determinations of the lactic acid and CO_2-content of the blood showed that also for very great work intensities which are accompanied by considerable washing out of lactic acid, reliable R.Q.-values may be obtained 10 to 15 minutes after the start of work.

Literature

Bnag, O., These Archives 1936, 74, Suppl. 10,51.
Boje, O., ibid., 1935, 71,61
Enghoff, H., ibid., 1935, 58,1.
Hansen, O., and A. Krogh, ibid., 1935, 71, 221.
Krogh, A., and J. Lindhard, Biochem. J. 1920, 14, 290.

II. STUDIES ON THE CATABOLIC PROCESSES DURING SEVERE MUSCULAR WORK OF LONG DURATION

E.H. Christensen and O. Hansen**

Possible sources of energy for muscular contraction are the three major nutrients: protein, carbohydrate, and fat. According to Liebig, protein alone should perform these functions. Studies by Pettenkofer and Voit (1866) have, however, shown that under normal conditions muscular work has no clearly demonstrable effect on the normal nitrogen output, findings which by and large have been confirmed. Subsequently, numerous authors have made the statement that the amount of energy required for muscular contraction might originate from carbohydrates. Chauveau (1896) found in his experiments on man an R.Q. of approximately 0.95 during work, the corresponding average R.Q. during rest was only approximately 0.75. Chauveau concluded from that, that the main source of energy for muscular work would be carbohydrates and made furthermore the assumption that fat could only serve as source of energy after its conversion to carbohydrates. This in turn, on the basis of theoretical considerations, means a loss in energy of approximately 30%. /152*

Experiments by Zuntz and co-workers (1896 and 1901) produced results which could not be brought in agreement with the assumption of Chauveau. These authors found that the R.Q. during muscular work as well as the R.Q. during rest depended upon the diet, for instance, during extreme fat diet values were found for the R.Q. during work which indicated almost complete catabolism of fat; these authors were also unable to demonstrate the great differences in the degree of efficiency for fat and carbohydrate metabolism which according to Chauveau had to exist.

The entire question received new interest when the muscle-chemical investigations of Fletcher, Hopkins, A.V. Hill and co-workers, Hill & Meyerhof (1923) made it likely that the energy delivering process during muscular contraction had to be the degradation of carbohydrate to lactic acid. /153

The discrepancies between the theory and the findings of Zuntz and co-workers induced Krogh and Lindhard (1920) to new studies of this

---

* Numbers in the margin indicate pagination in the foreign text.

** (From the Laboratory for the Theory of Gymnastics and the Laboratory of Zoophysiology of the University of Copenhagen)

(With 3 Figures in the text)

question. Like Zuntz, Krogh and Lindhard also found a close relationship between the R.Q. during rest - that is diet - and the R.Q. during work. On the basis of a refined technique, Krogh and Lindhard were able to further demonstrate that the degree of efficiency during fat metabolism was not lowered by 30% as had been assumed by Chauveau but only by about 10%. These results were in essence confirmed by Bierring (1931) who carried out his determinations also shortly after the start of work.

The investigations just mentioned of Krogh and Lindhard, and also those by Bierring, were conducted at low intensities of work. It was ascertained that the work lasted sufficiently long so that a steady state was reached. These investigations did not, however, allow firm conclusions on the relationships during great intensity of work. The experiments of Bock, Dill, and co-workers (1928) have, however, subsequently shown considerable differences in the metabolic processes during low and high intensities of work. It was made likely that a relationship between intensity of work and R.Q. is in existence, i.e., for highest intensities of work values for the R.Q. were found which were close to 1.0 and indicated a percentage increase in the turnover of carbohydrate. The experimental results of Bock, Dill, and co-workers were confirmed by Christensen (1932), who, however, doubted whether on the basis of these R.Q.-values during work one was entitled to draw firm conclusions on the metabolic events during very high intensities of work. Christensen stressed the fact that simultaneously with an increase in R.Q., very frequently also a strongly increased ventilation per liter of O_2 will be found and that the increase in R.Q. could be eventually explained by an increase in CO_2-output as a consequence of strongly increased ventilation.

The possibility of washing out of CO_2 during severe work requires exact control of the experimental conditions, because only for a constant CO_2-content of the body during the period of determination definite conclusions from the determined R.Q. on the metabolic events are allowed. /154
In the following series of experiments we have attempted to determine R.Q.-values also for very high intensity of work in such a way that conclusions on the catabolic events are possible (1938, I).

Experimental Results

The following determinations were made with three well trained subjects, O.B., O.H., and M.N. The intensity of work was 1120 kgm/min. which corresponds to an O_2-uptake of approximately 2.4 to 2.9 liters/min. The trained subjects were able to carry out the work for 2 to 3 hours. The washing out of CO_2 in the first minutes of work was very low for these three subjects at this extent of work and of short duration. In the following discussion, however, the R.Q.-values of the initial 15 minutes of work are not taken into consideration, since, however, the work was conducted over periods of two to three hours without interruption, it was possible to carry out numerous Douglas determinations in the same experiment. In all cases the initial period was sufficiently long and the subjects were experienced from previous experimental series with valve respiration.

The subjects, on the days of experiments, had taken no meals and lived otherwise on a freely chosen mixed diet which was not controlled.

The dots in Figs. 1,2, and 3 show the course of the R.Q. values during work in two experiments at a work of 1120 kgm/min. For O.B. and M.N. maximum duration of work was 160 minutes, for O.H. 180 minutes. All three subjects show a distinct decrease in R.Q.-values in the course of the working period.

The values during work for O.B. are distinctly higher than the corresponding values during rest (0.78); approximately 15 min. after the start of work, i.e. definitely during the "steady state" period one finds R.Q.-values of approximately 0.84 and in the course of the following 90 minutes one observes a decrease to approximately 0.81; this value then is approximately constant to the termination of work.

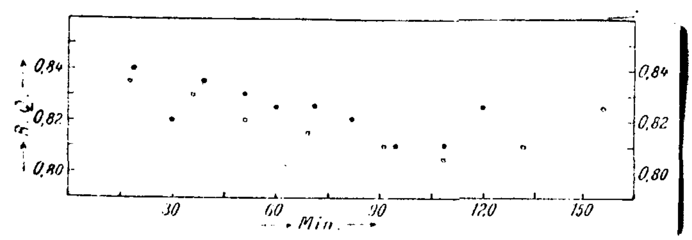

Fig. 1. Subject O.B., Work Intensity 1120 kgm/min. R.Q. during Rest = 0.78.

/155

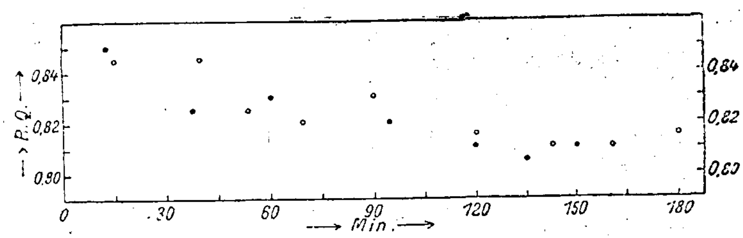

Fig. 2. Subject O.H. Work Intensity 1120 kgm/min. R.Q. during Rest = 0.86.

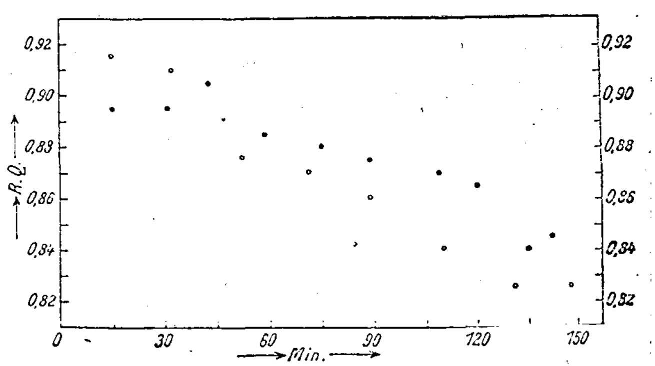

Fig. 3. Subject M.N. Work Intensity 1120 kgm/min. R.Q. during Rest = 0.81.

The R.Q.-values during work for O.H. are insignificantly higher than those for O.B. However, by comparison with the corresponding value during rest (0.86), the values during work are considerably lower; between 120 and 180 minutes after the start of work the R.Q. is here at a constant level of 0.81.

Subject M.N. (R.Q. during rest 0.81) shows R.Q.-values during work which are considerably higher than those for the other two subjects, in particular at the start of the working period. The decrease in R.Q. in the course of the working period is very considerable from approximately 0.91 to approximately 0.83, 150 minutes after the start of work.

A more detailed analysis of the different functions is presented in tables 1, 2, and 3. The values for R.Q. and the O_2-uptake are average values of the same experiments as in Figs. 1, 2, and 3. The duration of work is divided into periods of 30 minutes and the values given for the O_2-uptake and R.Q. refer to the mid-point of the 30 minute periods. With the help of these R.Q.-values, the percentage proportion of carbohydrate and fat calories has been calculated. Besides these values for metabolism /156
the blood sugar at the start of the periods is given.

Table 1. SUBJECT O.B. 1120 KGM/MIN.

Min. after the start of work	0-30	30-60	60-90	90-120	120-150	150-160
Liters of O_2 per minute.	2.71	2.75	2.75	2.83	2.92	2.93
R.Q.	0.835	0.825	0.820	0.815	0.810	0.810
Cal. % from carbohydrate.	43	40	38	36	34	34
Cal. % from fat.	57	60	62	64	66	66
Blood sugar mg%	86	82	78	73	56	52

Subject O.B. shows in the course of the working period an increase in the O_2-uptake from 2.71 liters/min. to 2.93 liters/min. This increase is very pronounced at the termination of work. The catabolism of fat and carbohydrate calculated with the help of the average R.Q.-values shows a decrease of the carbohydrate metabolism at a corresponding increase in fat metabolism during the course of work. The catabolism of carbohydrate contributes approximately 45% of the total energy in the course of the first 30 minutes of work, while at the termination of work only approximately 35% are contributed by carbohydrates. For O.B. the entire carbohydrate consumption was approximately 200 grams and the fat consumption approximately 250 grams.

The blook sugar values show during the first two hours a weakly decreasing tendency. After two hours, the total carbohydrate consumption was approximately 150 grams. Thereafter, a steep decrease follows and when the work was terminated the blood sugar had reached the low value of 52 mg%.

Table 2. SUBJECT O.H. 1120 KGM/MIN.

Min. after the start of work	0-30	30-60	60-90	90-120	120-150	150-183
Liters of O_2 per minute.	2.70	2.75	2.78	2.81	2.86	2.93
R.Q.	0.845	0.835	0.825	0.820	0.810	0.810
Cal. % from carbohydrate.	47	43	40	38	34	34
Cal. % from fat.	53	57	60	62	66	66
Blood sugar mg%.	123	117	110	118	107	100

Subject O.H. shows the same increase in metabolism during the course of work as subject O.B. and approximately the same R.Q.-values and therefore a similar percentage distribution between fat and carbohydrate catabolism. However, the blood sugar values are different. Subject O.H. /157
shows also decreasing blood sugar values during work, however, the decrease is not as pronounced. In particular, one does not find the steep decrease for the last few minutes of work and hypoglycemia. Despite a duration of work of 180 minutes and a total carbohydrate consumption of 235 grams the final blood sugar value was 100 mg% (fat catabolism approximately 170 g).

Table 3. SUBJECT M.N. 1120 KGM/MIN.

Min. after the start of work	0-30	30-6)	60-90	90-120	120-150	150-162
Liters of O per minute.	2.30	2.45	2.51	2.63	2.70	2.68
R.Q.	0.910	0.890	0.875	0.855	0.840	0.825
Cal. % from carbohydrate.	69	63	57	50	45	40
Cal. % from fat.	31	37	43	50	55	60
Blood sugar mg%.	84	84	75	83	86	66

Subject M.N. in particular shows during the early part of work a minor O_2-consumption, i.e., a higher efficiency than the other two subjects. The R.Q.-values are relatively higher than for subject O.B. and subject O.H. and after 160 minutes of work the carbohydrate consumption was approximately 270 grams. (Fat consumption approximately 100 grams). The blood sugar values at the start of work are comparable with those for subject

O.B. The decrease is, however, less steep, and the blood sugar at the termination of work was 66 mg%. Subject O.B. as well as subject M.N. were during the final period of work rather tired and showed weak symptoms of hypoglycemia.

Discussion

The experimental results reported show that the three trained subjects upon increase of the metabolism during rest by a 10 to 12 fold value were able to carry out a work of 1120 kgm/min. for hours. The entire total production of calories was 2000 to 2500 calories which were released upon catabolising 100 to 170 g of fat and 270 to 200 g of carbohydrate.

While a catabolism of fat of this order of magnitude affects the fat depots only to a minor extent the consumption of carbohydrate of 200 to 300 grams represents an extraordinarily significant decrease of the carbohydrate depots of the body. The low blood sugar values which were determined at the termination of work are a very definite sign for the fact that the quantities of carbohydrate which can be mobilized were decreased to such an extent that normal regulation of the blood sugar value was no longer possible. The eventual conversion of fat to carbohydrate shall /158
not be discussed in any greater detail since the experiments can not answer this question unequivocally.

Zuntz and co-workers (1901) and Krogh and Lindhard (1920) found a close relationship between R.Q. during muscular work and the extent of carbohydrate in the body. The decrease in R.Q. in the course of the first hours of work, which was found in the experiments just reported, is certainly an expression for reduced carbohydrate supplies as a consequence of the extensive consumption. It is, however, striking, that also at the termination of work where the carbohydrate supplies are certainly very low - the normal blood sugar regulation failed - that then, still a considerably carbohydrate consumption took place, approximately 40% of the energy originates from carbohydrates. The R.Q. in no case drops below 0.80. Despite the danger of serious hypoglycemia, the working organism continues to use, thus, still considerable quantities of carbohydrates and catabolic material although calories from fat were available in larger quantities.

Thus, one finds results which are no longer in agreement with the opinion just expressed. In the experiments reported here a significant carbohydrate consumption, in all likelihood, was a compelling necessity. Only upon catabolising this quantity of carbohydrates per minute, were the subjects able to perform this high intensity of work. The assumption that the intensity of metabolism is of great significance for metabolic events during work is thus supported by these experiments.

A closer analysis of this situation was the aim of the following series of experiments. The easily accessible depots were varied by unilateral fat or carbohydrate diet and by the intake of large quantities of calories and for low and high intensities of work, the relationship between metabolic events, extent of depots, intensity of work, duration of work, and influence of training under controlled experimental condition were studied.

Summary

Three well-trained subjects worked to the point of exhaustion at an intensity of work of 1120 kgm/min. The duration of work was 160 and 180 minutes. The total production of calories amounted to 2000 to 2500 calories which were released upon catabolizing 100 - 170 g of fat, and 270 - 200 g of carbohydrate. The R.Q.-values showed for all three subjects an increase in fat catabolism in the course of the working period. Also at the termination of work, when the carbohydrate supplies are very low - for one of the subjects blood sugar values of 52 mg% were determined - still /159
approximately 40% of the energy were contributed by carbohydrate. Despite the danger of serious hypoglycemia the working organism utilizes at this intensity of work still considerable quantities of carbohydrate while calories derived from fat were available in larger quantities. These results indicate that the R.Q. during work is not solely a function of the available carbohydrate depots and support the assumption that the intensity of work and also the intensity ofmetabolism have a decissive effect on the type of catabolic events during work.

III. ABILITY TO WORK AND NUTRITION

E.H. Christensen and O. Hansen**

The following series of experiments represent detailed studies on the significance of a diet rich in carbohydrate and one rich in fat, respectively, for the metabolism during work, and in particular, for the ability to work during work of long duration. The following three types of diet were applied. 1. normal diet (N) with carbohydrate and fat content in approximately isodynamic quantities, 2. diet rich in carbohydrate (C-H), where approximately 90% of the calories were derived from carbohydrate, and 3. diet rich in fat (F) where only approximately 5% of the calories originated from carbohydrate. The total intake of calories originated from carbohydrate. The total intake of calories in all cases amountedto 3500 to 5000 calories per day. The protein content was low, for the normal diet and carbohydrate diet approximately 60 g, and for the fat diet only approximately 20 g per 24 hours. In the case of the fat diet the protein content was kept so low in order to obtain R.Q.-values as low as possible. /160*

Table 1 shows the diet for a carbohydrate day.

All three subjects tolerated the extreme carbohydrate diet very well, only the intake of the large quantities of calories caused certain difficulties so that for the main meals it took more than one hour before the quantities offered had been eaten.

An example of a "fat day" follows in Table 2.

In addition to the calory-rich fats, here for reasons of digestion, vegetables were given of low calory content and, as a rule, also smaller doses of alcohol, approximately 15 cc of C_2H_5OH per day. This diet was tolerated.

The three trained men O.B., O.H., and M.N. were again the subjects of these experiments. The carbohydrate and fat experiments were always placed between periods with normal diet. /161

---

* Numbers in the margin indicate pagination in the foreign text.

** (From the Laboratory for the Theory of Gymnastics and from the Laboratory for Zoophysiology of the University of Copenhagen)

TABLE 1

September 14, 1932, Subject O.H.

Carbohydrate Diet

			Protein	Fat	C-H	Cal.
1.	Breakfast (8:00 AM)					
	pearl barley	100 g pearl barley	10	1.2	69	336
	rhubarb desert	360 g rhubarb desert	2	0.4	130	544
			12	1.6	199	880
2.	Breakfast (12:00 noon)					
	carrots, potatoes and	285 g carrots	4	1.3	54	250
	flour sauce with	275 g potatoes	4	0.0	54	238
	parsley	170 g bananas	2	0.2	21	100
	rice-pap with rhubarb	100 g rice	6	0.4	80	357
	desert	30 g wheat flour	3	0.4	23	118
	white bread with	20 g white bread	2	0.5	11	58
	bananas	360 g rhubarb desert	2	0.4	130	544
	Carlsberg beer	300 cc beer	0	0.0	34	199
			23	3.2	387	1864
3.	Lunch (5:00 PM)					
	pearl barley with	100 g pearl barley	10	1.2	69	336
	apricot desert	70 g whole grain bread	4	1.7	36	180
	whole grain bread	105 g white bread	8	3.9	58	307
	and white bread	170 g bananas	2	0.2	21	100
	tomatos, bananas,	150 g tomatos	1	0.2	7	33
	honey	260 g apricot desert	6	0.3	56	340
		30 g honey	0	0.0	21	88
			31	7.5	268	1384
4.	Supper (8:00 PM)					
		70 g white bread	5	2.6	39	204
		40 g honey	5	0.0	29	118
			5	2.6	68	322
	Total intake on September 14:		71	15.0	922	4450

In the first series of experiments (with subject O.B.) the carbohydrate and fat periods lasted only 3 days each with daily work experiments on the bicycle ergometer. This was sufficient in order to obtain pure fat catabolism during rest (R.Q. = 0.71), however, during carbohydrate periods R.Q.-values were obtained which did not exceed 0.89. Since it was also difficult in the subsequent series of experiments with M.N. to obtain high R.Q.-values, the diet periods were extended to one week and work was only performed every other day. For the two subjects M.N. and O.H. now also R.Q.-values of 0.95 were determined; by contrast, during the fat period the R.Q.-values were not lower than 0.74.

On each day of experiment the metabolism during rest was determined in the morning before means were eaten. The subject sat in comfortable position in an arm chair. /162

The determinations of metabolism were carried out according to the helmet technique as suggested by Hansen and Krogh (1935). Two determinations during rest of 15 minutes duration each were always carried out in direct succession. The result of these two determinations showed on the average a deviation of approximately 1%; in no case was the difference greater than 3%.

For O.B. and M.N. the normal duration of work on days of training was 60 minutes at 1080 kg/min. and the metabolism was determined according to the helmet technique between 10 and 15, 35 and 40, and 55 and 60 minutes after the start of work. For O.H. the duration of work was 120 minutes and the determinations of the metabolism were between 20 and 30, 50 and 60, 80 and 90, 110 and 120 minutes after the start of work. On the last day of experiments with extreme diet, work was conducted to the point of total exhaustion (determinations of the metabolism were carried out each 30 or 60 minutes). The duration of work in these experiments is a direct expression for the ability to work during long duration of work.

The nitrogen output was not determined and the protein-free R.Q.-values during rest are calculated under the assumption that the protein turnover calculated for 24 hours, was equal to the intake of the previous day. The work values do not show protein corrections for the calculation of calories consumed, since the correction of the R.Q.-values would amount to less than 0.003. The calculation of calories was based upon the data of Cathcart and Cuthbertson (1927).

Figures 1-3 show the trend of the R.Q.-values for different types of diet in the course of the working period. The dots of the curves (N) show average values of the R.Q. for all experiments and for mixed diet. As in earlier experiments, O.H. shows initially and R.Q. of 0.840 and during the course of work a minor decrease to 0.815. The other two subjects showed a distinctly higher R.Q. at the start of work (R.Q. = 0.88) and the decrease was very steep, so that after one hour an R.Q.-value was determined of approximately 0.84.

TABLE 2
September 25, 1932, Subject O.H.

Fat Diet

			Protein	Fat	C-H	Cal.
1.	Breakfast: coffee with whipped cream	2 dl whipped cream (30%)	4	62	7	608
2.	Breakfast: mayonnaise with tomatos	mayonnaise	3	69	5	671
	porridge with butter	150 g tomatos	1	0	7	33
	rhubarb with whipped cream	90 g porridge	2	0	4	24
		80 g butter	0	67	0	629
		rhubarb	1	0	5	24
		1 dl whipped cream (30%)	2	31	3	304
			9	167	24	1685
3.	Lunch: cauliflower with butter	100 g cauliflower	2	0	6	34
	bacon with apples	80 g butter	0	67	0	629
	apples and cream	215 g bacon	4	189	0	1772
		50 g apples	0	0	5	20
		1 dl whipped cream (30%)	2	31	3	304
			8	287	14	2659
	Total intake on September 25:		21	576	45	5073

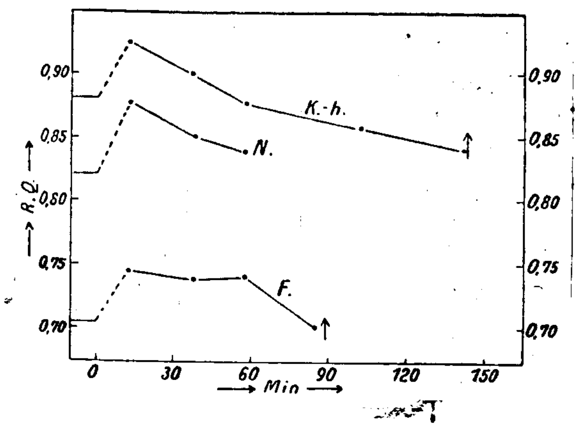

Figure 1. Subject O.B. Work intensity 1080 kg/min. K-h = carbohydrate; N; R.Q. during work after diet rich in carbohydrate. N; R.Q. during work after mixed diet. F; R.Q. during work after diet low in carbohydrate but rich in fat. -termination of work. In the N - and carbohydrate experiment this subject did not work to the point of complete exhaustion.

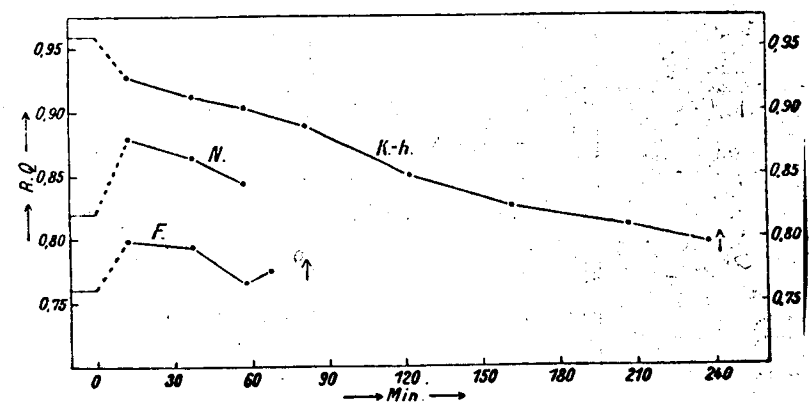

Figure 2. Subject M.N. Work intensity of 1080 kg/min. carbohydrate, N, and F, explanation cf. Fig. 1. -termination of work. In the carbohydrate and fat experiment work was conducted to the point of complete exhaustion.

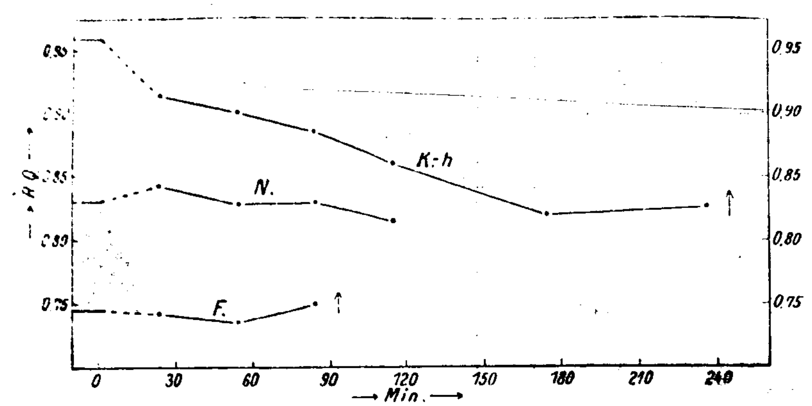

Figure 3. Subject O.H. Work intensity 1080 kg/min. carbohydrate, N. and fat, explanation cf. Fig. 1. -termination of work. In the carbohydrate and fat experiment work was conducted to the point of complete exhaustion. /164

TABLE 3

O.B. R.Q. during rest = 0.880. Work intensity 1080 kg/min.

Minutes after the start of work	0-30	30-60	60-90	90-120	120-150
O_2-Uptake (liter/min.)	2.63	2.71	2.75	2.76	2.85
R.Q.	0.925	0.890	0.870	0.855	0.845
Carbohydrate catabolism %	75	63	56	50	47
Fat catabolism %	25	37	44	50	53
Blood sugar (mg %)	70	72	70	70	60

Total carbohydrate catabolish 285 g.

The average R.Q.-values during rest for normal diet were for O.H. 0.83, for O.B. and M.N. 0.82. The percentage ratio between carbohydrate and fat catabolism during work was thus, as in earlier experiments, for O.H. the same as during rest, while O.B. and M.N., in particular during the earlier portion of the working period, showed an increase in carbohydrate catabolism.

The carbohydrate curves represent the R.Q.-values for three carbohydrate experiments of long duration. All three subjects show here almost the same reaction. The first R.Q.-values during work are approximately 0.92; this is followed by a continued decrease until termination of work. For O.H. and M.N. work was carried through to the point of exhaustion for a duration of work of more than four hours. For M.N. finally an R.Q. below 0.80 was determined; O.H. worked during the last 60 minutes with an R.Q. of 0.82. It is possible that the last value for O.H. is no longer reliable since after the termination of work a distinct acidosis could be demonstrated. The experiment with O.B. had to be discontinued after 150 minutes since the cooling of the helmet was not sufficiently effective. O.B. was not exhausted.[2]

The average R.Q.-values for carbohydrate diet were for O.B. 0.88, for M.N., and O.H. 0.96. The percentage ratio between carbohydrate and fat catabolism during work showed for O.B., as in earlier experiments with mixed diet, a shift in favor of the carbohydrate catabolism in the earlier part of the working period. /165
For M.N. and O.H. who showed very

[2] In this case the duration of work is not an expression for the ability to perform work.

TABLE 4

O.B. R.Q. during rest = 0.960; work intensity 1080 kg/min.

Minutes after the start of work	0-30	30-60	60-90	90-120	120-150	150-180	180-210	210-240
O_2-Uptake (liters/ min.)	2.31	2.40	2.39	2.41	2.43	2.46	2.54	2.65
R.Q.	0.925	0.910	0.890	0.865	0.840	0.825	0.815	0.800
Carbohydrate catabolism %	75	69	63	54	45	40	36	31
Fat catabolism %	25	31	37	46	55	60	64	69
Blood sugar (mg %)	75	80	70	73	79	70	65	59

Total carbohydrate catabolism 370 g.

TABLE 5

O.H. R.Q. during rest = 0.960; work intensity 1080 kg/min.

Minutes after the start of work	0-30	30-60	60-90	90-120	120-150	150-180	180-210	210-240
O_2-Uptake (liters/ min.)	2.48	2.51	2.52	2.59	2.61	2.65	2.69	2.73
R.Q.	0.915	0.900	0.890	0.870	0.875	0.825	0.820	0.825
Carbohydrate catabolism %	71	66	63	56	47	40	38	40
Fat catabolism %	29	34	37	44	53	60	62	60
Blood sugar (mg %)	95	95	95	95	97	97	88	86

Total carbohydrate catabolism 400 g

high values for the R.Q. during rest, however, the first values during work were considerably lower, approximately 0.92. Thus we find here in accordance with Krogh and Lindhard (1920) that the R.Q. during work does not reach extremely high values despite the fact that certainly very considerable carbohydrate depots are available.

In Tables 3-5 we have compiled various determinations made in the course of the working period. The O_2-uptake showed, as in earlier experiments, a continued increase. The carbohydrate and fat catabolism calculated on the basis of the R.Q.-values mentioned above show that in the course of the first 30 minutes carbohydrate contributed approximately 75% of the energy and fat the remaining 25; during the last minutes of work, however, approximately 60 to 70% originate from fat catabolism and only 30 to 40% from carbohydrate. The entire carbohydrate consumption was in the course of the 240 minutes for O.H. 400 g and for M.N. 370 g. The blood sugar values for these two subjects were in the course of the first 180 minutes almost unchanged, for M.N. between 70 and 80 mg%, and for O.H. between 95 and 97 mg%. In the course of the last 60 minutes a decrease follows for O.H. to 86 mg%, for M.N. to 59 mg%. This indicates undoubtedly that the carbohydrate depots for M.N. were almost exhausted and also for O.H., in all likelihood, that sizable carbohydrate quantities were no longer available. /166

The shorter duration of work for O.B. (150 min.) caused a carbohydrate consumption of 285 g and the blood sugar showed at the termination of work a decrease to 60 mg%. Blood sugar regulation was also here not sufficiently effective, presumably due to low carbohydrate depots which were already indicated by the relatively low R.Q.-values during rest.

The curves (F) of the figures show the R.Q.-values of the fat experiments of long duration during which the work could only be conducted for 80 to 90 minutes. The two subjects O.B. and O.H. here show an R.Q. during work of approximately 0.74 in the course of the first 60 minutes of work. The final values immediately before the termination of work are somewhat deviating for O.H.; we find an increase in R.Q. of up to 0.75 while O.B. shows a decrease to 0.70. These two final values, in all likelihood, are not a definitive expression for the metabolic events; both subjects showed clearly acetonuria. For O.B. the final metabolic determination had to be reduced to two minutes since the subject was no longer able to carry out work. The third subject M.N. showed higher R.Q.-values, approximately 0.80 for the first determination and approximately 0.77 at the time of termination of work (approximately 80 minutes).

The average R.Q.-values during rest were for O.B. 0.705, for O.H. 0.745, and for M.N. 0.760. The two subjects O.B. and M.N. show here for the initial period of work higher R.Q.-values than during rest and the subject O.H. who is the best trained one showed also here almost no differences in R.Q. between "during rest" and "during work".

Tables 6, 7, and 8 represent the course of the O_2-uptake during the period of work. As opposed to the carbohydrate experiments O.B.,

TABLE 6

O.B. R.Q. value during rest = 0.705; work intensity 1080 kg/min.

Minutes after the start of work	0-30	30-60	60-90
O_2-Uptake (liters/min.)	2.74	2.78	2.77
R.Q.	0.745	0.740	0.720
Carbohydrate (catabolism %)	10	8	1
Fat (catabolism %)	90	92	99
Blood sugar (mg %)	80	66	64[1]

[1] Minimum after 45 minutes of work 59 mg%.

Total carbohydrate catabolism 30 g.

TABLE 7

M.N. R.Q. during rest = 0.762; work intensity 1080 kg/min.

Minutes after the start of work	0-30	30-60	60-90
O_2-Uptake (liters/min.)	2.57	2.58	2.57
R.Q.	0.795	0.780	0.770
Carbohydrate catabolism %	29	24	20
Fat catabolism %	71	76	80
Blood sugar (mg %)	76	72	61

Total carbohydrate catabolism 60 g.

shows only a minor increase in O_2-uptake, however, M.N. and O.H. show an increase of O_2-uptake of approximately 10%.

In line with the low R.Q.-values in these experiments almost the entire quantity of calories is contributed by fat catabolism, approximately 70 to 80% for M.N., and more than 90% for the other two subjects. Consequently, the entire carbohydrate consumption was low, for M.N. approximately 60 g, for O.H. approximately 35 g, and for O.B. approximately 30 g. This means, however, in all likelihood for all three subjects an almost complete depletion of the carbohydrate depots, since the blood sugar values at the termination of the experiments were 64 mg% for O.B., for M.N. 61 mg%, and for O.H. 70 mg%. At the termination of work all three subjects were completely exhausted.

TABLE 8

O.H. R.Q. during rest 0.747; work intensity 1080 kg/min.

Minutes after the start of work	0-30	30-60	60-93
O_2-Uptake (liters/min.)	2.63	2.72	2.75
R.Q.	0.740	0.735	0.750
Carbohydrate catabolism %	8	6	12
Fat catabolism %	92	94	88
Blood sugar (mg%)	84	80	70

Total carbohydrate catabolism 35 g.

SUMMARY

The experimental series reported have shown that the three trained subjects were able to work 2 to 3 times as long after carbohydrate diet than after fat diet. As a possible cause for the decreased ability to work during fat diet the low carbohydrate turnover, the low blood sugar values, and the acetone bodies in the blood have been taken into consideration. Two of the three subjects were able to carry out a work of 1080 kg/min. (O_2-uptake of approximately 2.75 liters/min) for 90 minutes at an R.Q. below 0.75; more than 90% of the energy was contributed by fat catabolism.

APPENDIX I

Fig. 4 is a graphic representation of the relationship between R.Q. and metabolism during rest (O_2-uptake). Subject M.N. shows the lowest O_2-uptake for the highest R.Q.-values (0.22 liters/min. at R.Q.-values between 0.90 and 0.95); for lower R.Q.-values the O_2-uptake increases and is for R.Q. 0.80 equal to 0.23 liters/min.. This increase corresponds very closely to the reduced caloric value of oxygen and the production of calories in this interval is constantly at 1.11 calories per minute. Only for the lowest R.Q.-values the O_2-uptake increases more strongly than corresponds to the decreasing caloric value of oxygen.

For subjects O.B. and O.H. for R.Q. values above 0.8, no dependence between R.Q. and oxygen uptake can be shown. For low R.Q.-values, however, also here one observes a strong increase in the O_2-uptake; for O.B. the values are higher by 10%, for O.H. they are higher by 15% than for an R.Q. of 0.8.

Thus, one finds for all three subjects a distinctly increased O_2-uptake for the lowest R.Q.-values. This is in good agreement with the

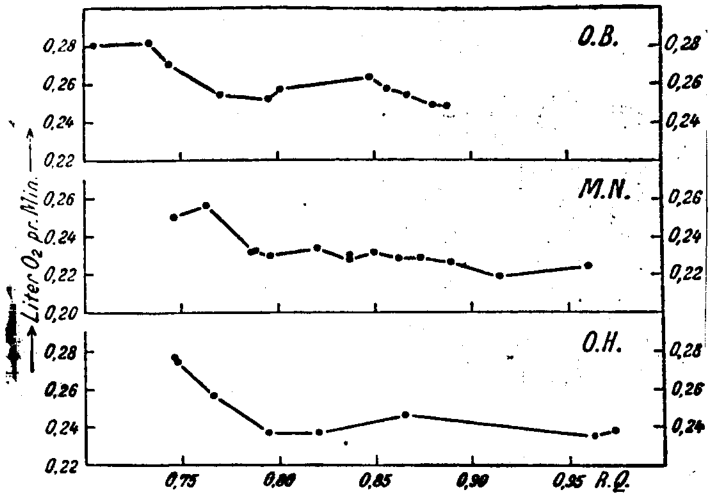

Figure 4. O_2-Uptake during Rest for Different R.Q.-values.

results of earlier investigators (Krogh and Lindhard (1920) and Bierring 1931)) where, however, the increase was only approximately 5 to 10%. A possible cause for the extra O_2-uptake is perhaps to be seen in a conversion of fat into carbohydrate (Krogh and Lindbard).

The increased O_2-uptake may perhaps also be explained by the fact that the oxydative degradation of fat at the low R.Q.-values must proceed by way of other reactions which cause an extra loss in energy (cf. for instance Blixenkrone-Moller (1938)). It appears, as is demonstrated in Table 9, that there is no relationship between the excretion of acetone bodies and the increase in the O_2-uptake.

TABLE 9

Date	R.Q.	Increase in the O_2-Uptake	mg Acetone per liter of urine
22.9.32	0.745	15%	15
24.9.32	0.760	8%	180
26.9.32	0.745	15%	350

APPENDIX II

The question of the relative efficiency for fat and carbohydrate as catabolic material during muscular work has been for a long time of central significance in the discussion of energy producing events during muscle contraction in general. Various investigators, however, arrived at rather different conclusions; however, by and large, the working hy- /170
pothesis offered by Krogh and Lindhard must be considered to be valid, i.e., during fat catabolism an extra loss in energy of approximately 10% takes place.

In Table 10 we have compiled the material reported here - although it was collected for an entirely different purpose - with regard to the production of calories during different catabolic events (intensity of work 1080 kg/min.). Table 10 contains the average values for the R.Q. and for the net-calory-production in experiments with extreme diet. The values were determined after a duration of work of 15 to 20 minutes. For the calculation of the net energy production a determination of the metabolism during rest on the same day was used.

TABLE 10

Subject	Number of experiments	R.Q.	Net-energy-production calories/min.
O.B.	3	0.920	11.90
"	3	0.780	11.50
M.N.	5	0.910	10.65
"	12	0.815	11.15
O.H.	3	0.915	10.95
"	3	0.765	11.15

The two subjects M.N. and O.H. show the lowest production of calories in the carbohydrate period, while O.B. shows the lowest value during fat diet. For O.B. the relatively low production of calories presumably can be explained by the better state of training during fat experiments. In the experiments with normal diet the subject O.B. showed a pronounced training effect. In the first experiment the production of calories was 12.2 cal/min. and in the last experiment of this series 11.2 cal/min., i.e. a difference of approximately 10%. For M.N. and O.H. the training effect was much smaller. The results of the experiments with M.N. and O.H. thus support the assumption of Krogh and Lindhard; the number of experiments, however, is small and the variation of the R.Q.-values not sufficiently great in order to draw definitive conclusions.

LITERATURE

Bierring, E. Arbeitsphysiol. 1932, 5, 17.

Blixenkrone-Moller, N., Ketonstoffernes Stilling og Betydning i det intermediare Stofskifte. Diss. Copenhagen 1938.

Cathcart, E. P. u. D. P. Cuthbertson, J. Physiol. 1931, 72, 349.

Hansen, O. and A. Krogh, These Archives 1935, 71, 221.
Krogh, A. and J. Lindhard, Biochem. J. 1920, 14, 290.

IV. HYPOGLYCEMIA, ABILITY TO WORK, AND EXHAUSTION

E. H. Christen and O. Hansen**

Preceding series of experiments (1938, III) had shown that trained subjects were able to work 2 to 3 times as long at an intensity of work of 1080 kg/min. after carbohydrate diet than after fat diet. As a possible cause of the poor ability to work upon fat diet the following has to be considered: the low carbohydrate turnover, the low blood sugar value, and the acetone bodies in the blood. In order to analyse these circumstances more closely, the following series of experiments with carbohydrate intake were carried out. /172*

a. Experiments with sugar intake during work.

Two or three days before the experiments the diet of the two trained subjects O.B. and M.N. was in essence free of carbohydrate in order to have glycogen depots as low as possible already at the start of work. Work was carried out on Krogh's bicycle ergometer at a work intensity of 1080 kg/min..

Upon almost complete exhaustion and during uninterrupted work 200 g of glucose dissolved in water were taken.

Figures 1 and 2 show the O_2-uptake, R.Q., and blood sugar values of these experiments. The curves of Fig. 1 represent the results of an experiment with O.B. after two days of fat diet. The O_2-uptake was approximately 2.0 liters/min. and the corresponding R.Q.-values were 0.80 to 0.81. The blood sugar curve shows 160 minutes after the start of work a decrease from approximately 90 mg% to approximately 60 mg% (total carbohydrate consumption 155 g). At this time the subject was exhausted and showed unequivocally sumptoms of hypoglycemia. At this point 2 x 100 g of glucose dissolved in water were taken and approximately 15 min. af- /173
ter the begin of the sugar intake the subject noticed the favorable effect. The hypoglycemic symptoms disappeared and the subject worked without difficulties for another hour.

The curves for O_2-uptake and R.Q.-values do not show a distinct influence of the sugar intake; however, the blood sugar curve shows, as was expected, a steep increase to approximately 100 mg; after the termination of work a renewed increase could be observed.

---

1 For greater detail on these experiments with sugar intake cf. O. B Boje 1935.

* Numbers in the margin indicate pagination in the foreign text.

** From the Laboratory for the Teory of Gymnastics and from the Laboratory for Zoophysiology of the University of Copenhagen.

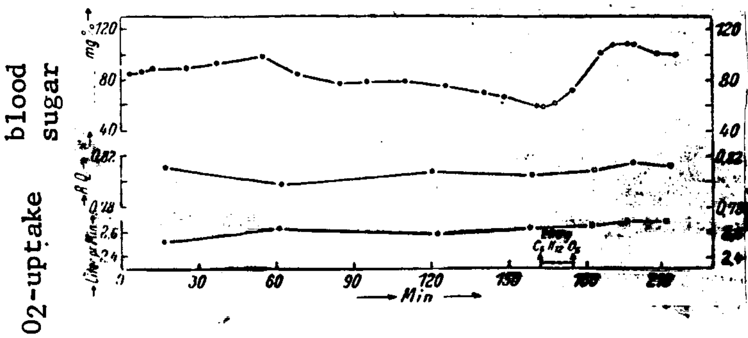

Figure 1. Subject O.B. blood sugar, R.Q., and O_2-uptake. Work intensity 1080 kg/min. 200 g glucose; o determinations before, o determinations after the intake of sugar.

The curves of Fig. 2 show the results of a corresponding experiment with M.N.. As was usually the case, the O_2-uptake for this subject was very low, 2.4 to 2.5 liters/min. The R.Q. was higher than for O.B., 0.82 to 0.83. The blood sugar curve shows a decrease from approximately 80 mg% to approximately 51 mg% after 120 min. (total carbohydrate consumption at this time 135 g). The subject was almost completely exhausted.

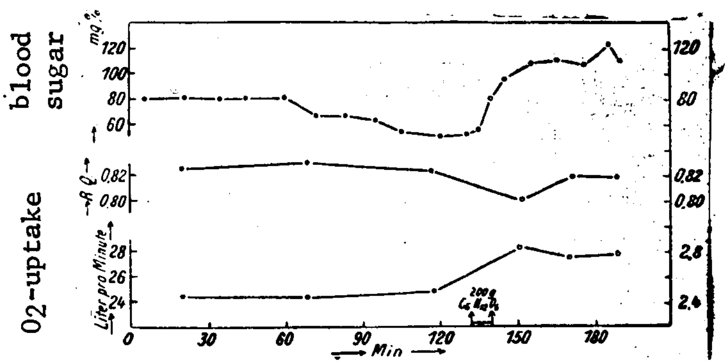

Figure 2. Subject M.N. Explanation cf. Fig. 1.

The intake of glucose after 130 minutes renewed /174
ability to work and work could be continued for as long as 190 minutes. The curve for the O_2-uptake here shows a distinctly higher level after the sugar intake, but the R.Q. again is not affected. The blood sugar curve shows a steep increase to 110 mg % already after 30 minutes of the intake of sugar. Upon discontinuation of work another steep increase to 180 mg % takes place. Unfortunately, glucose excretions in urine was not measured.

b. Sugar intake before work.

Subsequent to the series of experiments just discussed, experiments were conducted with metabolism and blood sugar determinations after identical sugar intake during rest; 160 to 180 minutes after the sugar intake work of identical intensity as earlier was initiated. Figures 3 and 4 show the results of these determinations.

The blood sugar values for O.B. show an increase from 100 mg% to a maximum value of 175 mg% 25 minutes after the sugar intake. Thus, the increase was somewhat faster and greater than in the working experiment mentioned earlier. After approximately 135 minutes the blood sugar curve shows subnormal values of approximately 80 mg%. Work was begun after 158 minutes and the blood sugar curve shows a very minor increase at the time of termination of work.

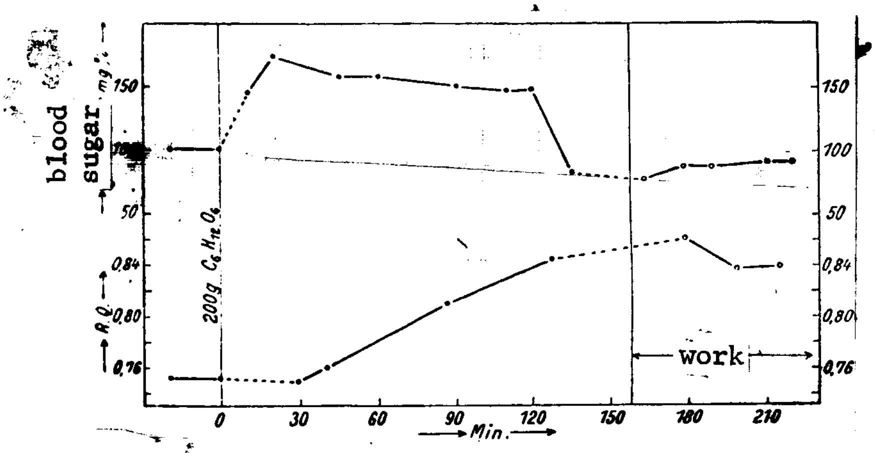

Figure 3. Subject O.B. blood sugar and R.Q. during rest and during work after sugar intake during rest. Work intensity 1080 kg/min.

The R.Q. curve shows an increase 40 minutes after the sugar intake and after 120 minutes a value of 0.85 has been reached which represents an increase of 0.10. Approximately 20 minutes after the start of work an R.Q. of 0.86 was determined and the subsequent determination after 40 and 60 minutes showed values of approximately 0.84. When the work was terminated subject O.B. did not show any signs of exhaustion. /175

Subject M.N. shows a very great increase in blood sugar values. From approximately 80 mg% the curve reaches 60 minutes after the sugar intake a maximum of 230 mg%. Thereafter this is followed after 175

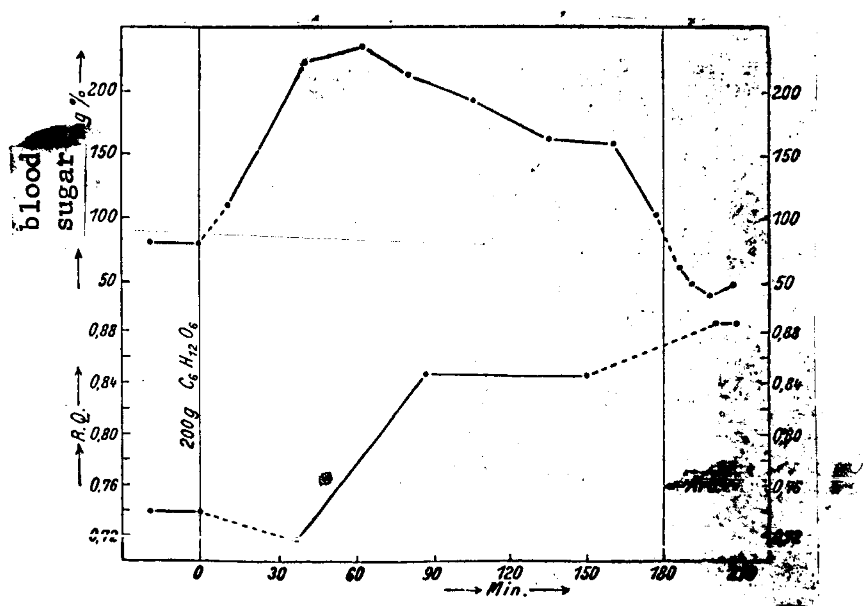

Figure 4. Subject M.N. Explanation cf. Fig. 3

minutes by a decrease to approximately 100 mg%. Work was started 180 minutes after the sugar intake and a further decrease in the blood sugar values was observed; 17 minutes after the start of work the blood sugar had reached the extremely low value of 40 mg%! The subject now was completely exhausted and work could only be continued for 27 minutes under greatest concentration and under pronounced psychic disturbances. The last blood sugar determination showed a value of 48 mg%.

The first R.Q. determination 35 minutes after the sugar intake shows a decrease of 0.74 to 0.72. The following determinations after 85 and 150 minutes show the constant value of 0.85. The determination during work shows an R.Q. of 0.89.

DISCUSSION

The experimental data have shown considerable independence between the R.Q. and the blood sugar value. Even one hour after sugar intake during work hardly a visible increase in the R.Q.-values could be demonstrated, despite the fact that the blood sugar curve had reached maximum values already after approximately 30 minutes. (cf. Boje 1935)). This corresponds to the findings of Dill and coworkers (1932) and Atzler, Lehmann and Szakall (1937). By contrast, Carpenter and Fox (1931), and Carpenter and Lee (1933) found that the R.Q. during rest already 30 minutes after sugar intake was increased and upon work of lesser intensity, Carpenter and Fox (1931) observed a corresponding effect; upon greater intensity of work (555 kg/min.), however, no effect of the sugar intake on the R.Q. could be demonstrated; work was, however, discontinued already after 30 minutes because of exhaustion. /176

The blood sugar curves presented show the normal steep pattern during rest, while during work the quantitative effect of the sugar intake on the blood sugar level is of lesser degree. This corresponds, among other things, to the findings of Strandell (1934) and Atzler, Lehmann, and Szakall.

According to Courtice and Douglas (1936) and Mills (1938), however, the blood sugar increase may be very great after extensive work performance if excessive sugar supplies are available during restitution.

The lesser slope of the blood sugar curve after sugar intake during work may be attributed to different causes, namely 1) a particularly rapid event of deposition, 2) to a lesser degree, however, to increased carbohydrate consumption in working muscles, 3) a possible delay in sugar resorption during work as a consequence of a strong decrease in intestinal circulation.

The fact that Carpenter and Fox (1931) and Carpenter and Lee (1933) observed after sugar intake during work and during rest an earlier effect on the R.Q. than we, is probably related to a difference in the degree of filling the glycogen deposits at the time of sugar intake.

In the case of small carbohydrate depots the "tendency of deposit" is dominant perhaps as opposed to catabolic events and only if a certain carbohydrate quantity has been deposited an increase in catabolism begins. In a similar way we probably must interprete the results of Atzler, Lehmann and Szakall (1937). In experiments of long duration with dogs a distinct effect of the sugar intake on the R.Q. can only be observed for high doses of sugar.

The almost complete independence of the catabolic events and blood sugar level must indicate that the glucose quantities administered can not be utilized directly as catabolic material but rather that first a conversion to glycogen in the working muscles has to take place.

The unusual situation where upon sugar intake during rest serious hypoglycemic symptoms occurred during work, may probably be represented in the following way: subsequent to the sugar intake during rest, resorption begins in a normal fashion and the blood sugar increases already after 10 to 15 minutes. After 60 minutes the blood sugar curve reaches a maximum and the usual decrease begins. This decrease indicates that resorption now provides less sugar to the blood than is simultaneously deposited and catabolized. The blood sugar curve eventually reaches subnormal values and subsequent to that an increase to normal values follows. If now, during the period of low blood sugar values, severe work will be initiated, this then means absolutely and eventually also relatively an increase in carbohydrate consumption. In the present experiment the working R.Q. was = to 0.89. In the earlier experiment without sugar before work, the working R.Q. was equal to 0.83. The carbohydrate provided, thus, has here increased the percentage carbohydrate conversion in the working muscle and since simultaneously a strong tendency to deposit is prevalent, the result is a very strong decrease in blood sugar. Here one then observes the paradoxial case that subject M.N. as a result of the intake of 200 g of glucose, due to severe hypoglycemic symptoms, was unable to carry through with the work. The regulatory mechanism had failed. The hypoglycemia due to work must in this case be considered the result of a relative insufficiency of the mechanism for carbohydrate mobilization.

In the experiments reported as well as in earlier series of experiments there is a close relationship between the ability to work and subnormal blood sugar values. The restoration of the ability to work in the experiments with sugar intake during work was timewise related to the increase in blood sugar values. Whether, however, the blood sugar level is of decisive significance for the energetic events in the working muscles can not be concluded with certainty from these experiments.

The values for the O_2-uptake and the R.Q. nevertheless indicated that the metabolism during work was quantitatively and qualitatively very little influenced by sugar intake; but a barely demonstrable effect of the increased sugar level on the metabolism in muscles can not be /178
denied. The renewed ability to work could be attributed to a minimal

increase of the carbohydrate turnover in the working muscles and a decrease in the accumulation of acetone bodies.

The experiment with M.N., in which the sugar was given three hours before work and in which fatigue was observed 15 minutes after the start of work, now demonstrates clearly that the increase in carbohydrate turnover in the working muscle in itself did not favorably influence the ability to work. In these experiments carbohydrate turnover was considerable, the R.Q. during work was 0.89 and an accumulation of acetone bodies can not be considered seriously. The O_2-uptake of 2.47 liters per minute was quite normal and the strong and well-trained subject was usually able to carry out work of 1080 kg/min. for hours without showing symptoms of exhaustion. The only cause that could be demonstrated for the fact that fatigue occurred already 15 minutes after the start of work is the low blood sugar level. The immediate cause for exhaustion can, however, hardly be found in the muscles. Much more likely - as had already been assumed by Boje (1935) - fatigue is of cerebral origin. The normal function of the central nervous system can not be coordinated with the low blood sugar values and fatigue from work must, therefore, in this case be looked upon as a hypoglycemic symptom of nervous origin. Since the central nervous system can only utilize carbohydrate as energy-delivering material, it is in itself not surprising that the tolerance to decrease the blood sugar values here is probably much lower than it is in muscles. The central nervous system is also much less tolerant toward low oxygen tension than are muscles.

SUMMARY

The experiments have demonstrated unequivocally - as has already been found earlier - that sugar intake during low blood sugar values improves the ability to work considerably. The improved ability to work can, however, not be explained by the renewed carbohydrate availability in the muscles, because only an increase in the blood sugar level due to this availability of carbohydrate shows a favorable effect. Thus, the favorable effect is certainly not the result of increased carbohydrate depots, or of a percentage increase in carbohydrate catabolism in the muscles, but rather exclusively that of higher blood sugar level and is closely related with the disappearance of the hypoglycemic symptoms. Exhaustion must be interpreted as a hypoglycemic symptom of cerebral origin.

LITERATURE

Atzler, E., G. Lehmann and A. Szakall, Arbeitsphysiol. 1937, 9, 579. /179
Boje, O., These Archives 1936, 74, Suppl. 10, 1.
Carpenter, T. M., and E. L. Fox, Arbeitsphysiol. 1931, 4, 570.
Carpenter, T. M., and R. C. Lee, J. Nutrition 1933, 6, 55.
Christensen, E. H., and O. Hansen (III), These Archives 1939.

Courtice, F. C., and C. G. Douglas, Proc. roy. Soc. B. 1936, 119, 381.
Dill, D. B., H. T. Edwards, and I. H. Talbott, J. Physiol. 1932, 77, 49.
Mills, J. N., ibid. 1938, 93, 144.
Strandell, B., Acta med. Scand. 1934, 55 Suppl., 245.

Translated by Translation and
Interpretation Division of the
Institute of Modern Languages
Washington, D. C.